J. Physiol. (1953) 119, 170–190

SPECTRAL SENSITIVITY AND WAVE-LENGTH DISCRIMINATION OF THE PERIPHERAL RETINA

By R. A. WEALE

From the M.R.C. Group for Research in the Physiology of Vision, Institute of Ophthalmology, London

(*Received* 16 *June* 1952)

The unqualified success with which the human scotopic sensitivity function has been explained in terms of the absorption spectrum of visual purple (Trendelenburg, 1904; Hecht, 1921) has prompted visual physiologists to seek further instances of parallelism between sensory phenomena on the one hand and objective observations on the other. The latter cover such widely different fields as the photochemistry and optical properties of retinal pigments, the histology and electrophysiology of the retina, and the anatomy of the visual pathways.

The question of pigments is of the utmost interest because it is generally thought that, once definite photosensitive substances become associated with the human retinal cones in the same way as visual purple is associated with rods, a major step will have been made towards the solution of the problem of colour vision. It is further argued that if parallelisms can be established between the retinal spectral faculties, expressed in terms of the stimuli, and photosensitive pigments respectively, a decisive blow may be struck for or against a particular theory of colour vision. In this connexion, the retinal periphery occupies a key position, because, in the absence of any knowledge of cone pigments, the visual sensations experienced in the extrafoveal parts of the human retina have been invoked to oppose the trichromatic theory of Young and Helmholtz. Such colour experiments as have been carried out on the retinal periphery cannot be compared with work done on the fovea, as the control of the experimental conditions has been inadequate. There is, therefore, a good reason why the spectral faculties, known in such detail for the fovea, should be examined in the periphery and proper controls applied to the investigation.

Secondly, the structure of the retina has already revealed the parallel

between rods as associated with twilight vision and cones as linked with daylight vision. Histological studies have also shown that, whereas the central fovea is rod-free, no part of the periphery is cone-free. Thus colour vision in some form or other would be expected to be present throughout the periphery. Moreover, it would be interesting to know whether the activity of the rods affects it in any way. This point has not been covered adequately in connexion with the fovea, let alone the periphery. Unless, for example, the rods are completely inactive at low *photopic* luminance levels, colour vision, measured at such levels, might be expected to be trichromatic in persons usually called dichromats. In consequence, a possible parallel between retinal structure and colour vision would be helpful towards the understanding of the visual mechanism.

In the third instance, the visual sensations and the anatomy of the visual pathways have also provided some parallelisms. The best known of these is Le Gros Clark's suggestion (1949) to the effect that the lamination of the lateral geniculate body is topographically conjugate with the retina and that the fusion of the laminae 4 and 6, 3 and 5 is the physical counterpart of the predominance of the yellow sensation in the peripheral retina. Hartridge (1949), however, has given some valid criticisms of this view. Another parallelism, apparently unconnected with peripheral colour vision, yet one worthy of mention because of the technical difficulties which it causes in its exploration, exists between the relative lack of importance of the messages conveyed to the brain from the retinal periphery and the small size of the cortical visual areas associated with the periphery (Holmes, 1945). At first sight it is paradoxical that the small area of the fovea should carry such weight in the interpretation we give to our foveal visual sensations. However, the disparity between the foveal and peripheral projections on the cortical visual areas, which is so much in favour of the former of the two, provides a simple explanation of this phenomenon.

At the same time, this disparity provides a reason why work on the periphery has been neglected by most workers interested in colour vision. It gives rise to the enormous difficulty of foveally fixating a spot, however minute, and simultaneously observing events in the periphery, however well marked. This iso-retinal rivalry has no counterpart in foveal observations. Other reasons for the paucity of data on peripheral colour vision are of a physiological and physical nature. Thus the image of an external object formed by the ocular dioptric system on the peripheral retina is ill-defined because of several aberrations. The perception of such an image is rendered even more difficult owing to the decrease of visual acuity with perimetric eccentricity: this is due to the increasing complexity of the arborizations of the peripheral neurones. In addition, after-images persist longer in the periphery than in the fovea, thus rendering the observations still more

difficult; and, unless the observations are relatively short, temporary insensitivity may set in: one can 'stare' with the fovea but not with the periphery.

Severe though some of these difficulties might appear, an investigation of colour vision in the retinal periphery seemed worth undertaking for the reasons mentioned above. A first step towards the elucidation of some of the problems connected with this subject was taken by measuring the spectral sensitivity and wave-length discrimination at retinal eccentricities of 0, 10 and 15° (Weale, 1951*a*, *b*). The measurements have now been extended to locations of 25, 45 and 70° off the fixation area in the temporal visual field of the observer's left eye: an effort was made to reach 80°, but, with the existing experimental arrangements, no observations could be made at this location. The retinal positions so far investigated are shown in Fig. 1.

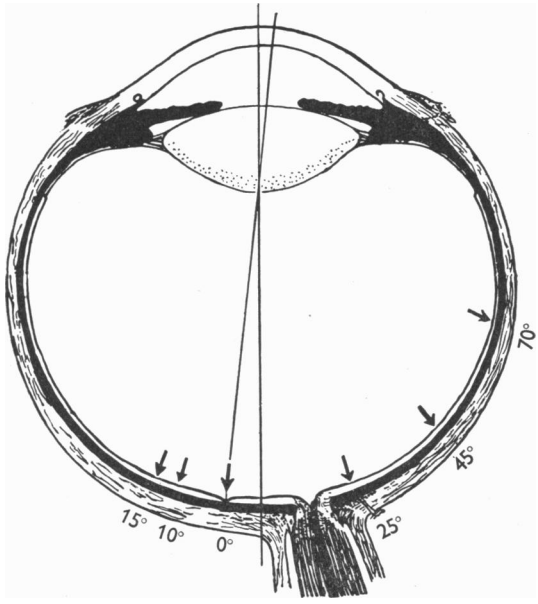


Fig. 1. Horizontal section of the eye showing the retinal locations to which the present measurements refer.

METHOD

Apparatus. The experimental arrangement was similar to the one previously described (Weale, 1951*a*, *b*). Two circular fields, *A* and *B*, subtending at the eye an angular diameter of 50′ were provided by the prism faces of two Hilger Barfit monochromators. The entrance slits of the latter were illuminated by a single 6V 18A tungsten ribbon filament lamp whose voltage was kept constant by a 'Westat' constant potential power unit and by manual control of a rheostat. Scattered light was reduced by using Ilford Bright Spectrum filters (621–6, 608–9) at the appropriate wave-lengths. The brightness of the fields was controlled by neutral filters and wedges. The fields were in Maxwellian view, images of the exit slits of the two monochromators being formed in the plane of the observer's pupil.

There appeared several points peculiar to visual measurements in the retinal periphery. In the first instance, the eccentricity of the stimulated retinal area was determined by a minute red fixation spot. The observer's head was steadied with a firm mouthpiece carrying his dental impression: to obviate an effort on the part of the ocular muscles due to the large eccentricities of the test-fields *A* and *B*, the mouthpiece was turned approximately in the direction of fixation. Thus there was no need appreciably to turn the eyes towards the fixation spot. Secondly, the inevitable turning of the head about a vertical axis made it impossible to use an artificial pupil. However, as the exit-slits of the monochromators were optically conjugate with the observer's pupil, it was permissible to restrict them longitudinally so that their images, focused in the plane of the pupil, were smaller than the smallest pupillary diameter (2 mm). The removal of the original artificial pupil made it impossible to attach a separate correcting lens: the observer, therefore, had to wear his glasses. Thirdly, visual acuity deteriorates rapidly as the angular distance from the fovea is increased. In the previous work (Weale, 1951*a*, *b*) the two test-fields were separated by an angular distance of the order of ½°: they were only just distinguishable. The separation between them was considerably increased in the present experiments partly because a just distinguishable separation adds to the strain of the measurements and partly because the increased eccentricity stipulated an increased separation. The fields were vertically above each other, their centres being separated by 3° at a retinal eccentricity of 25°, and by 4° at 45° and 70° respectively. This made them more easily distinguishable than in the earlier experiments. Fourthly, in view of the peripheral situations of the retinal areas investigated, adequate control of the state of adaptation of the eye was imperative. The reason is because, in these regions, the number of rods is very large as compared with that of cones. Thus, if the eye were not light-adapted, cone vision might be dominated by rod-vision and the object of this investigation vitiated. It is obvious that a large rod density leads to easy dark-adaptation in the absence of light, and also that dark-adaptation had to be prevented from taking place. This was achieved by fitting a frame in front of the eye within the least distance of distinct vision. The frame carried two to four sheets of filter or other coarse-grain paper, which were perforated in two places to permit the passage of the test and fixation beams. One to three incandescent lamps were so arranged behind the screen as to illuminate uniformly the part of the paper in front of the eye. Since the screen was at a distance of only 2 in from the eye small irregularities in the paper were completely out of focus and passed unnoticed (Thomson, 1949). The number of layers of paper and the position, number and wattage of the lamps determined the intensity of illumination: this was measured with an Edgcumbe Photometer placed flat against the observer's side of the screen. The two luminance levels employed corresponded to 1·5 and 100 e.f.c. respectively, and will be referred to as *L* (low) and *H* (high). They were both above the photopic threshold. The adaptation of a retinal area of about 90° by 90° could thus be controlled.

Calibration of the apparatus. The wave-length calibration of both monochromators was carried out with Na, Hg and Cd vapour lamps. The neutral wedges and filters, and the relative energy transmitted by *A*, were calibrated with electron multiplier cells as before, the stray-light filters being used at the appropriate wave-lengths.

Positioning of the observer's pupil. This was achieved by adjusting the mouthpiece so that when the observer bit it the amount of light entering his eye from *A* and *B* was maximal. The two beams were made to coincide in the plane of the observer's pupil to eliminate the Stiles-Crawford effect (cf. Wright, 1946).

The observer's colour vision. The observer (R.A.W.) was 28 years of age. Except for slight refracting errors (corrected) he suffered from no disability. As indicated by his foveal wave-length discrimination and spectral sensitivity (Weale, 1951*a*, *b*) his foveal colour vision was normal.

Procedure. An assistant set the wave drums *A* or *A* and *B*, according to the nature of the experiment, to a wave-length of random choice. All subsequent operations were carried out by the observer. Thus in sensitivity measurements he matched the brightness of *A* to that of *B*; and in measurements of wave-length discrimination he changed the wave-length of *A* or *B*, keeping the brightness of the changing field equal to that of the other. The assistant then noted the result of

this measurement, and set the wave-drum(s) to another wave-length of random choice. The observer then made another setting. The whole of the spectrum was thus covered at intervals of $0{\cdot}1\phi$ ($1\phi = 10^{14}$ c/s; $x\phi = c/\lambda$, where c is the velocity of light, $2{\cdot}998 \times 10^{10}$ cm/sec, and λ the wave-length in μ). Owing to the normal lack of energy at short wave-lengths the requirement of constant luminance level results in the H measurements being fewer in number than the L measurements. The whole of the explorable spectrum was covered at one sitting of about an hour's duration, and two such sittings were held every day—one in the morning and one in the afternoon. With one or two exceptions, L measurements were taken during the morning and H measurements in the afternoon or vice versa. Such a distribution of the sessions, coupled with the randomization of the settings, tended to balance day-to-day variations. Their effect was also reduced by repeating each measurement several times. None of the measurements could be prejudged by foveal observation since, as soon as the eye was turned towards the test-fields, the beams struck the iris instead of passing through the pupil. As the object of the measurements was to determine certain characteristics of the light-adapted eye, colour vision being at its fullest at high luminances, the sessions were not preceded by periods of dark-adaptation. They gave rise to considerable physical strain which necessitated a brief period of rest after about 40 min. The observer found closing his eyes effective, but before taking subsequent readings he adapted them for ½ min to the illumination of the white screen providing the surround.

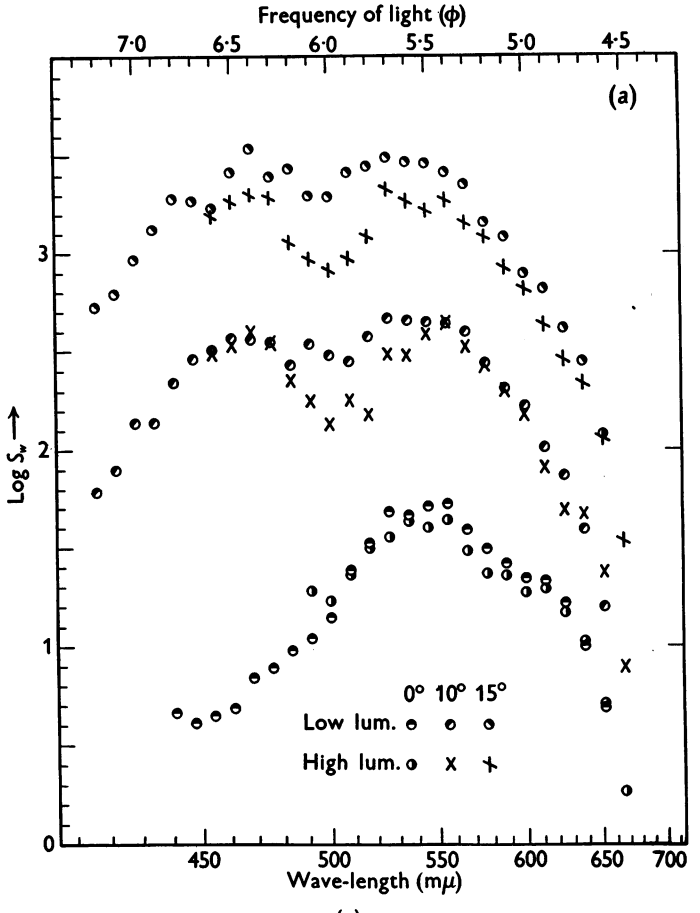
Measurement of spectral sensitivity. This was carried out by making a brightness match between the fields A and B; A was the test-field whose wave-length and brightness could be altered, B the comparison field, whose brightness was equated visually to that of the surround, and whose wave-length was kept at 563·6 mμ. This wave-length has no special significance except that, as viewed peripherally, it appeared to be achromatic; thus the difficulties due to chromatic differences encountered in heterochromatic photometry were reduced. The retinal location of 25° was investigated first, that at 45° next, and the one at 70° last. Seven observations were made for each location and each luminance level.

Measurement of wave-length discrimination. This visual faculty was measured in the usual manner: A and B were set to identical wave-lengths and their luminances independently adjusted to that of the surround. Then the wave-length (λ) of one of them was changed towards the red end of the spectrum ($\lambda + \Delta\lambda$) until a difference in hue could be perceived. This was measured by $\Delta\lambda$. At the same time the brightness of the changing field was kept constant. By altering the wave-length of first one field, say A, and, during another sitting, the other, values $\Delta\lambda_A$ and $\Delta\lambda_B$ were obtained. If there is a statistically significant difference between the mean values $\overline{\Delta\lambda_A}$ and $\overline{\Delta\lambda_B}$ where $\Delta\lambda$ represents the difference between the initial and final wave-length at each measurement, this may be interpreted as being due to the topographical component, i.e. due to the fact that the average spectral responses of the two receptor populations covered by A and B respectively are dissimilar because of a dissimilar distribution of receptors within them.

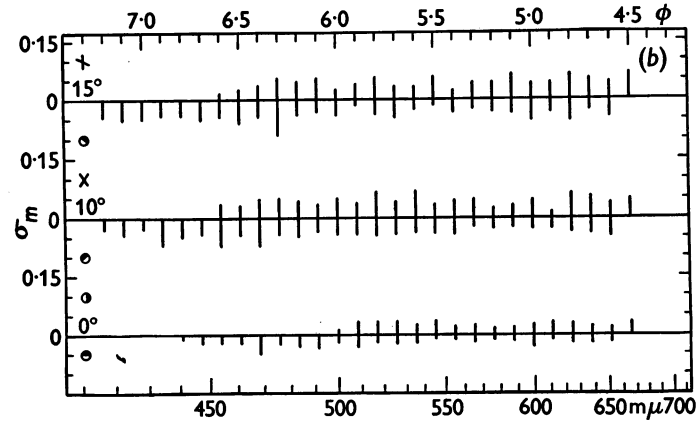
RESULTS

The new data, obtained for retinal locations of 25, 45 and 70° respectively, are shown with those obtained previously at 0, 10 and 15° (Weale, 1951*a*, *b*) so as to facilitate the comparison between them (Figs. 2*a*, 3*a*, 4*a* and 5*a*). Since the usual bars, indicating the standard errors of the mean σ_m, would only confuse the picture they have been plotted separately as a function of the wave-length, and are presented beneath the relevant graphs (Figs. 2*b*, 3*b*, 4*b* and 5*b*).

The sensitivity data (Fig. 3*a*) represent mean values of seven independent readings, obtained on different days. They were taken at two luminance levels (1·5 and 100 e.f.c.). The logarithm of the relative sensitivity S_w is plotted along the ordinate, the wave-length of light along the abscissa. The red end of the



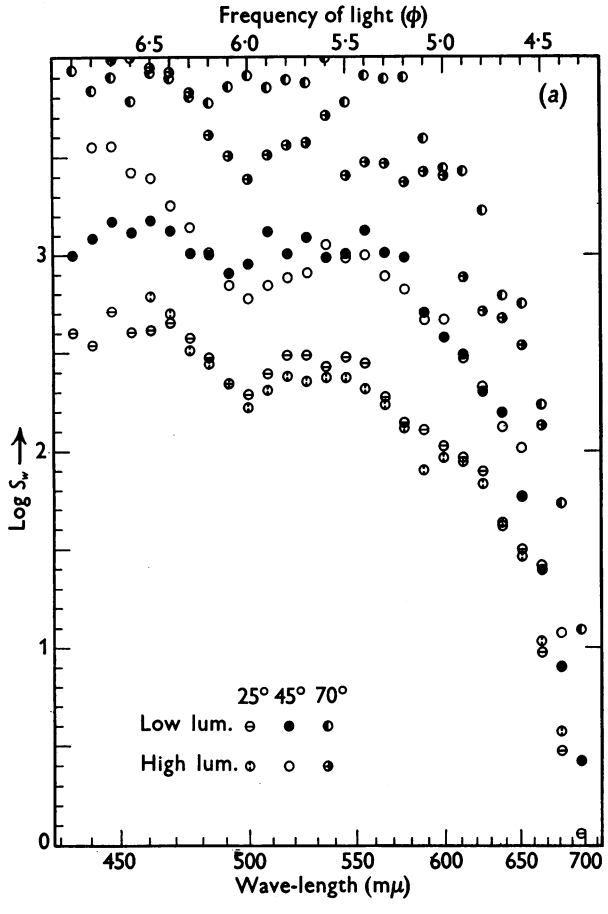
(*a*)



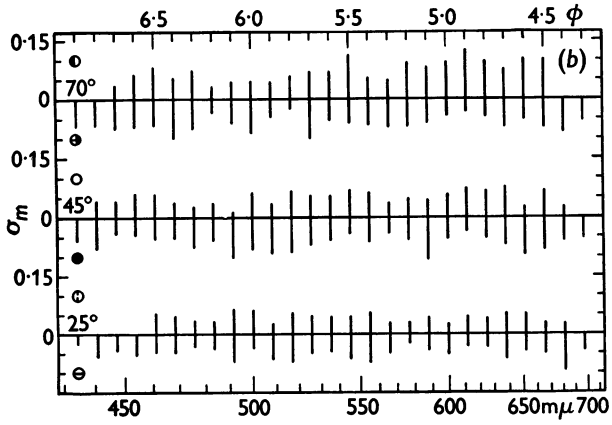
(*b*)

Fig. 2. (*a*) Logarithm of spectral sensitivity plotted against frequency. Red part of the spectrum on the right, violet on the left. (*b*) The corresponding standard errors of the mean.

	0°	10°	15°
Low luminance level (*L*)	◓	◐	◔
High luminance level (*H*)	◑	×	+



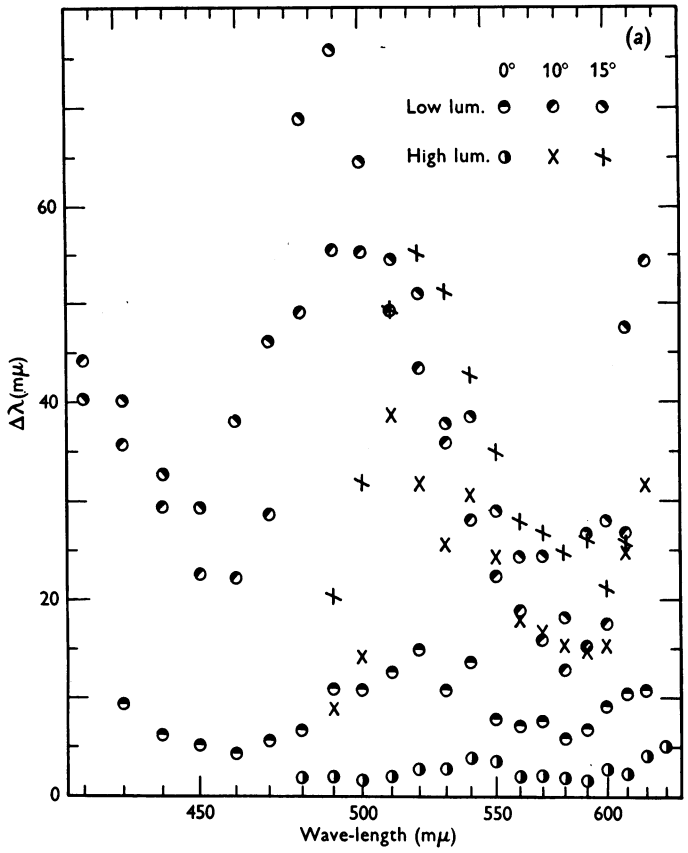
(a)



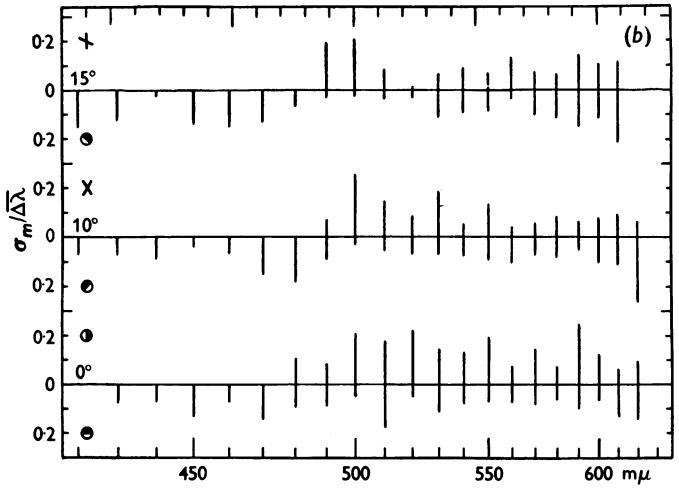
(b)

Fig. 3. (*a*) Logarithm of spectral sensitivity plotted against frequency. (*b*) The corresponding standard errors of the mean.

	25°	45°	70°
Low luminance level (*L*)	⊖	●	◐
High luminance level (*H*)	⊕	○	◑



(a)



(b)

Fig. 4. (*a*) Just noticeable wave-length step $\Delta\lambda$ in mμ plotted against wave-length. (*b*) The corresponding standard errors of the mean.

	0°	10°	15°
Low luminance level (*L*)	◓	◐	◔
High luminance level (*H*)	◑	×	+

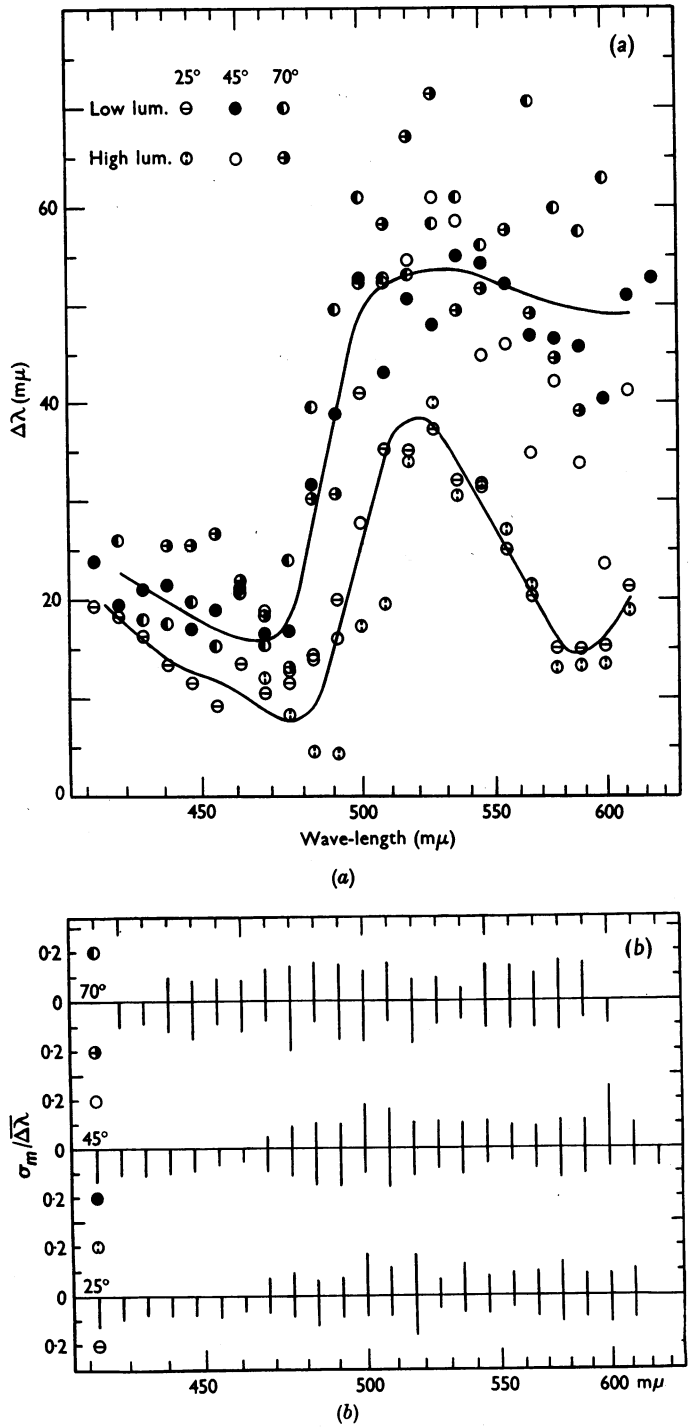


Fig. 5. (*a*) Just noticeable wave-length step $\Delta\lambda$ in mμ plotted against wave-length. (*b*) The corresponding standard errors of the mean.

	25°	45°	70°
Low luminance level (*L*)	⊖	●	◐
High luminance level (*H*)	⊕	○	◑

The lines are drawn by hand and indicate the difference between dichromatic and trichromatic characteristics.

spectrum is on the right, the violet on the left. No absolute measurements were made so that it was permissible to carry out relative displacements of each set of data along the ordinate: this facilitated comparisons between their general trends. The sensitivity results are plotted for an equal quantum spectrum, but no allowance has been made for the observer's glasses or absorption of light in the pre-retinal media. The curtailment of the data in the blue part of the spectrum is due to the usual lack of high frequency energy in the light source.

The results on wave-length discrimination (Fig. 5*a*) were obtained at the same luminance levels as the sensitivity data, namely 1·5 and 100 e.f.c. respectively. The steps, $\Delta\lambda$, are plotted along the ordinate, the wave-length λ representing the short-wave end of the step along the abscissa. As before, the violet end of the spectrum is on the left, and the red on the right. Each point represents the mean of ten independent determinations of the least perceptible difference in wave-length; five of these observations were obtained by changing the wave-length of the upper field *A*, giving rise to a value $\Delta\lambda_A$, and five by changing the lower field *B*, giving rise to one of $\Delta\lambda_B$.

The abscissa. Owing to the fact that the initiation of the visual act is normally of a photochemical nature, it is better to use a frequency rather than a wave-length scale along the abscissa. However, the latter has been hallowed by tradition, as has the fact that the violet part of the spectrum is on the left and the red on the right. It is impossible to satisfy both tradition and scientific theory, and therefore a compromise has been adopted in the present paper: the abscissal values were plotted in equal frequency intervals but calibrated in wave-lengths. This causes a relative congestion of the scale points on the right (red) side of each graph.

The accuracy of the data. Whereas the standard errors of the mean σ_m of the sensitivity S_w, as measured at retinal locations of 0, 10 and 15° (Fig. 2*b*), seem to show a systematic spectral variation (Weale, 1951*b*), this can no longer be observed in more peripheral parts (Fig. 3*b*). The larger values of σ_m may be responsible for this at least in part. The spectral variation of σ_m is, however, marked in the data on wave-length discrimination: σ_m is small when wave-length discrimination is good and vice versa. The errors are enormous in the central (green) region of the spectrum. It is thus more instructive to plot $\sigma_m/\Delta\lambda$ instead of just σ_m against λ (Figs. 4*b*, 5*b*).

DISCUSSION

Eccentricity. The eccentricity of the two fields *A* and *B* was measured at the obeserver's pupil. Since fixation was controlled by a luminous point of constant spectral composition, accommodation could not compensate for chromatic aberration. In the absence of any reliable data on the refractive errors of the

eye-media along optical paths leading to the retinal periphery, the wave-length of light which would be brought into focus peripherally under given conditions along the optic axis is unknown. Consequently a correction for the error involved by the spectral variation of the image size and the resultant error in the value of the sensitivity cannot be applied. It is, however, unlikely to be appreciable.

The topographical contribution to $\Delta\lambda$. A difference in hue between two fields can be produced by at least two factors: either the wave-lengths of the two stimulating fields are different, in which case the differential response of essentially similar receptor populations will be due to the difference between the component receptor groups, i.e. the cause is functional; or two equal stimuli may produce different responses because the mechanism populations within the two fields are dissimilar, i.e. the cause is topographical. These two effects are not mutually exclusive and may co-exist. Relative inhomogeneities in two mechanism populations will, of course, appear primarily if the two stimulus fields are small, and, as Thomson (1946) has shown, an effect, which can be explained on the above basis, is observed in foveal vision when the two fields subtend an angle of only 15′. Fields of 50′, as used in the present investigation, appear to be comparatively large when viewed foveally, but are subjectively minute in peripheral vision. Consequently, local differences in the mechanism mosaic might make themselves felt. This view is made more plausible if it is recalled that the cone density in the periphery is about one-third its foveal value: the linear dimensions of the present fields are about 3 times those used by Thomson.

The effect can be investigated by determining $\overline{\Delta\lambda}$ by changing the wave-length of A (the upper field) during one set of measurements, and that of B during another. Accordingly, half of the ten measurements for each value of $\overline{\Delta\lambda}$ (Fig. 5*a*) was obtained by each method respectively. The large errors, however, have made it impossible to detect the topographical component of $\overline{\Delta\lambda}$ except in isolated instances. In fact, they are so few and far between that it seems justified to combine into one mean value the two sets of five readings each, obtained by varying A and B respectively. On applying the t-test to $\overline{\Delta\lambda}_A$ and $\overline{\Delta\lambda}_B$, it was found that t was greater than 2·776, the value corresponding to a 5 % basis, only in the instances shown in Table 1.

TABLE 1. Statistically significant values of t, obtained on testing the differences between the means of $\Delta\lambda$, which resulted from changing the upper or lower field (A or B) respectively

Retinal positions	Luminance level	λ (mμ) 434·5	491·5	499·7	508·1	516·9	526·0
25°	*L*	—	—	—	—	2·98	—
45°	*L*	4·8	—	—	4·37	—	—
	H	—	—	—	—	—	3·15
70°	*L*	—	3·53	—	—	3·46	—
	H	—	—	4·91	—	—	—

The fact that the few statistically significant values of t are restricted to the short-wave part of the spectrum is, in all probability, due to the smaller absolute values of the errors. The standard errors shown in Fig. 5*b* are, however, worked out on the assumption that all the measurements for one point are distributed about one mean value, not about two. This accounts, for instance, for the vast error found for the L value at 499·7 mμ at 70°. While some of the t values in Table 2 are fairly large in comparison with 2·776, the general incidence of significant differences is very small. This failure to detect the topographical part of $\Delta\lambda$ may thus be due either to the large experimental errors or to the fact that the topographical component is too small to be discovered by the present experimental method.

Short-wave colour vision at great eccentricities. The remarkable relative sensitivity in the blue part of the spectrum which had appeared already at 10 and 15° (Fig. 2*a*) is even more pronounced at greater eccentricities: it is illustrated in Fig. 6 where the shapes of the sensitivities at 0 and 25° are compared. The red end of the foveal curve is relatively higher than that of the 25° if the two sets are equated at 555·2 mμ, the maximum of the foveal curve. But the 25° data are very much higher in the blue than are the foveal. The difference between these two curves in this region is so great that it cannot be accounted for by assuming that the foveal curve is depressed owing to absorption of light by the macular pigment. Wald's visual estimate (1949) of the maximum density of this pigment *in situ* is 0·6. In the present work measurements like Wald's lead to a value of approximately 0·7 when the retinal location is at 10 or 15°, a value of approximately 1·0 when it is 25°, 1·5 at 45°, etc. If the pigment is macular it is hard to see why its amount should be a function of a retinal location from which it is supposed to be absent. As a different argument has indicated (Weale, 1951*b*) the marked sensitivity to light of short wave-lengths, as measured in the periphery, must be due largely to the increased activity of a mechanism covering this part of the spectrum. The sensitivity data are here supported by those on wave-length discrimination (Fig. 5*a*). It is only in the blue part of the spectrum that good wave-length discrimination can be achieved. There is no evidence from foveal data that good sensitivity and wave-length discrimination occur in the same spectral regions: on the contrary, an elementary theory of wave-length discrimination (Wright, 1946) militates against this view. Again, the optimum in peripheral wave-length discrimination is at about 470 mμ (Fig. 5*a*), the peak of sensitivity at about 450 mμ (Fig. 3*a*). The latter would be moved to an even shorter wave-length if the correction for the absorption of light by the pre-retinal media were applied. The spectral distance between the optima in peripheral wave-length discrimination and sensitivity is thus of the same order as that between their foveal counterparts.

Variation of colour vision with luminance level. Fig. 7 compares the spectral

sensitivity at 45° as measured at a low and a high luminance level respectively. The data are juxtaposed by an arbitrary factor along the ordinates to facilitate comparison. The trough appearing at 500 mμ in the high luminance data is filled in, as it were, when the luminance level is lowered. This has also been observed at small eccentricities (cf. Fig. 2*a*). It could be due to an increased activity of the rods. However, while such a change is observed in the data for the sensitivity, a very different picture emerges when the luminance change is examined in connexion with wave-length discrimination. The differences between high and low luminance values have been calculated for both visual functions (Fig. 8). It is remarkable that wave-length discrimination should

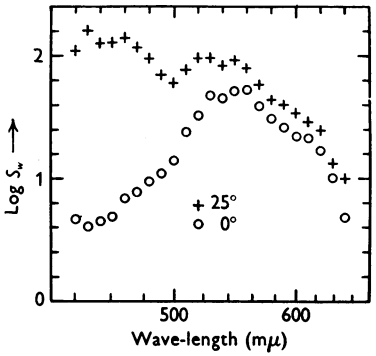


Fig. 6. Comparison between log S_w at 0° and 25° (L) plotted against frequency.

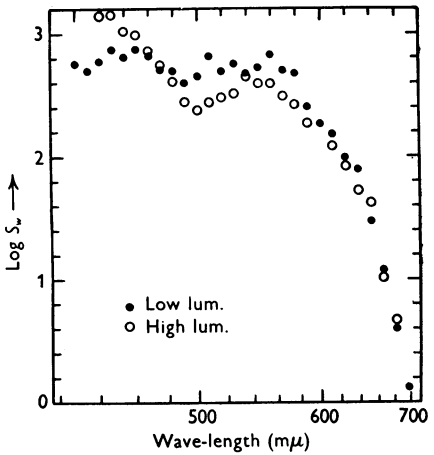


Fig. 7. Comparison between log $S_w(H)$ and log $S_w(L)$ at 45° plotted against frequency.

exhibit such a considerable deterioration at 500 mμ in the blue-green, whereas, by comparison, the changes in S_w are small. A similar observation was made at the smaller eccentricities of 10 and 15°. The rods are known to mediate luminosity at low (scotopic) luminance levels: their contribution to the perception of luminosity at higher luminance levels seems to be negligible. Yet marked changes in wave-length discrimination are taking place in their very region of activity. The deterioration of wave-length discrimination at lower levels seems to be due to desaturation, a fact previously observed by Lythgoe (1931). The magnitude of the errors in the wave-length discrimination data, however, results in statistically significant differences between the two luminance levels being restricted to the blue-green part of the spectrum for 25 and 45° (Table 2). If the differences in $\overline{\Delta\lambda}$ were due to chance then, on a 5 % basis, the value of t should not exceed 2·101.

Correlation between sensitivity and wave-length discrimination. Fig. 8 shows that there is hardly any parallel between the luminance variations of these two

visual functions. An examination of Fig. 5*a* reveals that the data obtained at 25° (like those at 10 and 15°, Fig. 4*a*) are characteristic of anomalous trichromatic vision. It is impossible to decide between protanomaly and deuter-

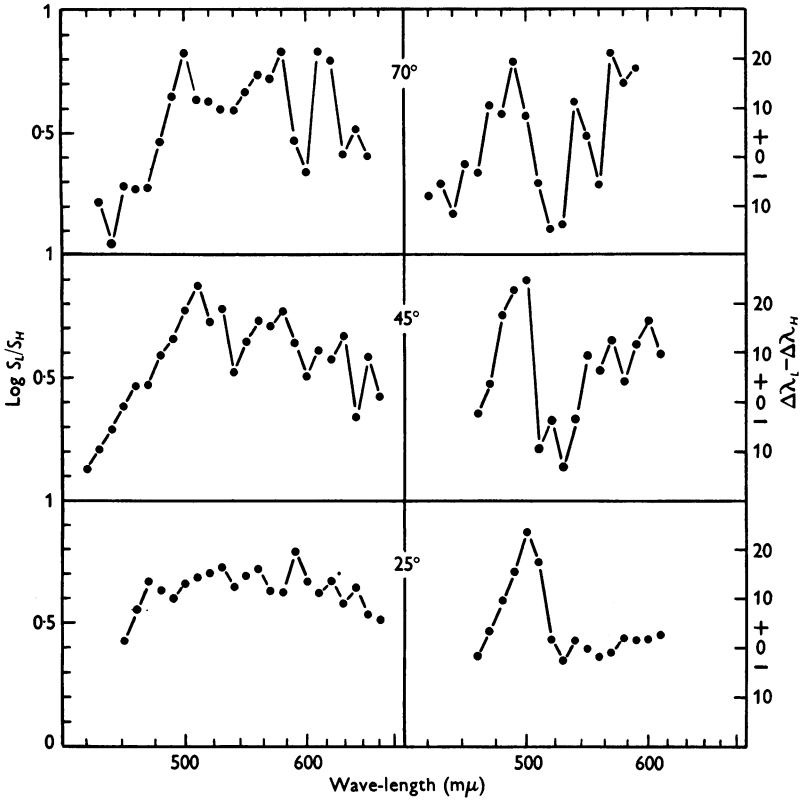


Fig. 8. The variation of spectral sensitivity S_w (left) and wave-length discrimination (right) with luminance level plotted against wave-length. The values for the high (*H*) are subtracted from those for the low (*L*) luminance level. The values for log S_w (low luminance) − log S_w (high luminance) are relative.

TABLE 2. Values of t obtained on comparing $\overline{\Delta\lambda}$ for the two luminance levels

	λ (mμ)				
Region	475·9	483·5	491·5	499·7	508·1
25°	2·42	5·38	8·58	5·15	4·18
45°	—	3·7	3·68	3·35	—

No statistically significant difference is obtained for the data at 70°.

anomaly in particular, because the short-wave optimum is at about 470 mμ instead of the usual 490–500 mμ. This shift may well be due to some form of tritanopia adding its effect. Hartridge (1947) has suggested that tritanopia would be observed in the normal eye whenever it was tested with a small

field, irrespective of the retinal location. On the other hand, a desaturating effect due to rods could also give rise to tritanopic characteristics (Gilbert, 1950). The variation of $\overline{\Delta\lambda}$ with luminance supports the latter view. Now if the data obtained for 45 and 70° are examined the characteristics of anomalous trichromacy are replaced by those of dichromacy. The errors and values of $\overline{\Delta\lambda}$ are very large, indeed, and the confusion at longer wave-lengths is pronounced.

The sensitivity data present another picture. The numerous kinks in Fig. 3*a* are, no doubt, due to experimental errors. But all the data show three well-marked humps in the orange, green and blue parts of the spectrum respectively. They appear at both luminance levels. While the orange hump is less pronounced at 10 and 15°, possibly because of less complete light-adaptation, statistical analysis has confirmed its presence in those regions. Just as their foveal counterparts (Thomson, 1951; Weale, 1951*b*), these humps have been revealed owing to the use of a small test-field. They are probably due to the same mechanisms as those in the fovea: their appearance in photopic spectral sensitivity data for retinal locations of 0, 10, 15, 25, 45 and 70° (Fig. 1) suggests that these mechanisms cover a major part of the retina. Now if three mechanisms appear to be present all over the retina, why does the periphery exhibit dichromatic characteristics? The problem is analogous to that presented by the central fovea: measurements of the spectral sensitivity reveal three mechanisms, while wave-length discrimination and colour-matching appears to be carried out with only two. Part of the answer seems to be provided by recent measurements on the foveal spectral sensitivity of a totally colour-blind cone-monochromatic subject. Even with a relatively large field (1° 20′) the brightness-matching revealed three spectral regions of enhanced sensitivity, in the blue-violet, green and orange respectively. Yet the subject had no trace of colour-perception, being able to make a perfect match between any two single spectral stimuli. This suggests that while the actual absorption of energy occurs in a triadic retinal mechanism, where also differentiation of colour takes place, a neurally posterior centre affects the perception of colour. The above result has been quoted as giving great support in evidence of Müller's (1930) zonal theory of colour vision. It provides a key to the understanding of the paradox presented by the apparent incompatibility of sensitivity and wave-length discrimination data, both foveal and peripheral. If a totally colour-blind subject possesses a tripartite luminosity function, it is hardly surprising that a normal subject should have a fundamentally similar function in regions of the retina which are partly colour-blind. The appreciation of colour is impaired foveally and peripherally owing to a failure of a centre other than the receptors and not largely because a pigment or receptor mechanism is missing.

Colour vision and retinal structure. Müller (1856) has suggested that the

retina should be divided into more or less well-defined regions, whose angular extents on the nasal side are as follows:

Foveal centre	50′	Inner periphery	14° 10′
Fovea	2° 30′	Intermediate periphery	24° 10′
Parafovea	4° 10′	External periphery	77° 35′
Perifovea	9° 10′	Ora serrata	80°

This division was arrived at by a consideration of the retinal anatomy and has recently been supported by Polyak (1941). When examining the relation between colour vision and the structure of the retina, the latter writer expressed the view that, since all foveal cones looked alike, it was improbable that the actual stimulus differentiation should take place in them: he mentioned the midget bipolar cells as possibly mediating the differentiation between colours. Contrary to accepted physiological and photochemical principles though this view may be, it is supported by a further remark of Polyak's, according to which the different shapes of the cones as the retinal periphery is approached may be associated with the supposedly parallel change in sensation. Thus, when the cones look all alike, a post-receptoral mechanism is used for differentiating between colours; but when they look dissimilar the work is done by the receptors. Results previously obtained on the foveal centre (Willmer & Wright, 1945; Thomson & Wright, 1947) have shown that this region is dichromatic and less sensitive to blue than is the fovea. According to Polyak himself the foveal centre is 'absolutely free of rods' and in the fovea there are only 'a few stragglers'. Yet with fields somewhat larger than 15′ in size there is no trace of any reduced sensitivity to blue even though the rod-free area is used (Weale, 1951*b*): it follows that the appearance of the cones provides no clue as to their function. On the other hand, normal subjects exhibit a regional variation in colour vision which can be summed up as follows:

	Type of colour vision	Sensitivity to blue
Foveal centre	Tritanopia	Reduced
Fovea	Trichromacy	Normal
Parafovea	Trichromacy	Enhanced
Inner periphery	Anomalous trichromacy	Enhanced
Intermediate periphery		Enhanced
External periphery	Dichromacy	Enhanced

There is thus no obvious correlation between retinal structure and colour vision: the rods considered as a twilight cell cannot be responsible for the sensitivity to blue in the fovea because their spectral response cannot explain the difference between the sensitivity of the foveal centre and the fovea as a whole. Also, according to Polyak, their foveal number is very small. None of the other structures are very helpful. It is a very curious fact that, although the human retina consists of ten layers, or eight if the limiting membranes are ignored, the explanation of colour vision has been sought in one of them to the

exclusion of all others. Thus even Polyak, who can conceive of post-receptoral mechanisms taking part in the colour-differentiating process, ascribes to one of them all the work in one part of the retina, namely the fovea, and relegates it to the cones in the periphery. The view put forward here is that, broadly speaking, the same process takes place all over the retina. Post-receptoral activity modulates the message. It is only because there are fewer centres of such activity in the more peripheral regions that the modulation is imperfect and can be made to compare with foveal standards by increasing the effective area of the intensity of the stimulus: both are means of bringing more of the peripheral centres into operation.

Comparison with other sensory data. Several reasons were given in the Introduction as to why the periphery should have been the Cinderella of colour vision. There are only three authors the conditions of whose work can be compared with those here discussed. Lythgoe (1931), as already mentioned, carried out a colour-naming test for the periphery. His qualitative conclusions in regard to desaturation at lower luminance levels, and the good recognition of blue throughout the periphery are supported by the present findings. Again, Stiles & Crawford (1933), ensuring that the periphery at 5° should be properly light-adapted, observed the tripartition of the sensitivity function in general and the short-wave increase in sensitivity in particular. Walters & Wright (1943) have not observed either of these phenomena when measuring the spectral sensitivity at a retinal location of 10°, a 2° field being employed. Their failure is probably due to the use of a surround of zero luminance and a relatively large test-field. Parsons (1924) gives a résumé of a number of older investigations on the peripheral spectral sensitivity at photopic luminance levels, but unspecified retinal locations. The maxima of some of these smooth, single-humped functions are in the yellow or orange part of the spectrum. Hartridge (1949) has taken this to mean that the periphery is characterized by a mechanism, the 'yellow receptor', particularly sensitive to this part of the spectrum. Unfortunately, for this view, these older data had not been corrected for the energy distribution of the various light sources used. When this is done they agree substantially with data obtained foveally. To quote from Parsons's book: 'On comparison of the peripheral photopic luminosity curve with König's and Abney's (foveal) luminosity curves, making allowance for the fact that the two former are with gas light, the latter with arc-light, we see that they agree.' This means that the equal energy correction moves the maximum to about 550 mμ. Such a shift seems incredibly large but becomes plausible when it is realized that König's foveal curve (Starling, 1949) has its maximum at 610 mμ and the application of the appropriate correction moves it to 550 mμ.

Peripheral colour sensations. Lythgoe (1931) has given a qualitative account of the variation of the colour sensations between the fovea and the extreme

periphery under conditions of both light- and dark-adaptation. The present writer concurs with it. From the point of view of measuring wave-length discrimination, however, the following additional point ought perhaps to be emphasized. The relatively good wave-length discrimination at shorter wave-lengths is due to a rapid change, not so much in the sensation of hue as in that of saturation. Thus, if *A* and *B* are blue, and *A* is changed towards the longer wave-lengths, the difference between the two is not that *A* becomes greener, but less distinctly blue and more nearly white. The red-green confusion is such that a field, seen as green foveally, is sometimes called orange when viewed peripherally. Similarly, a field seen foveally as orange, may appear as deep red in peripheral vision. It is frequently stated that yellow and blue are the two sensations which persist, under constant conditions, farther away from the fovea than any other. While it is certain that blue is recognized as such well into the periphery, the quality of yellow is doubtful. The present observer was only aware of a very desaturated sensation, due to an admittedly small field, and would have been at great pains to ascribe any colour-name to it: it may well be that because yellow is the most desaturated colour in normal foveal vision it experiences a smaller change than either red or green, and hence is said to be an invariable colour.

The relative enhancement of the sensitivity to blue light as observed in extra-foveal regions accompanies the above-mentioned saturation and is probably due to the eye being light-adapted (cf. Hunt, 1952). This was shown quantitatively in a dramatic way. The test-field *A* of wave-length 460 mμ was directed at the retinal periphery in the absence of the white surround. It appeared as a small desaturated blue field. Then the white surround was switched on. The above small desaturated field flashed as it were into a subjectively larger and much more saturated field. This change was instantaneous and more marked for the bright surround. Other hues were not similarly affected. The size effect is opposite to what is observed with white point images seen foveally (a 50′ field viewed peripherally can perhaps be compared with a point image seen foveally, cf. Rönne (1915)). Since this effect is absent from the fovea but present in the periphery, and rods likewise exist only outside the foveal centre, increasing in density with eccentricity (Østerberg, 1935), it is permissible to associate one with the other. The only objective experimental result supporting this view is Granit's observation (1947) that the guinea-pig's pure rod retina exhibits a modulator effect maximal at 460 mμ, and superimposed on the visual purple dominator when the eye is light-adapted. If the increase in the subjective size of the image is due to synaptic linkages, the improved saturation is unexpected (Hunt, 1950). On the other hand, it may be that 'saturated' colours can be perceived in the retinal periphery only if there is an adequate number of stimulated receptors. The variation of the colour-fields with the size and intensity of the test-field (Abney, 1913) and

observations made on colour-defective subjects lend some support to this hypothesis.

Conclusion

One of the objects of this investigation was to discover if there were any correlations between peripheral colour vision and other properties of the visual path. The expected effect of the rods on the sensitivity was not observed. Further, the shapes of the sensitivity curves were not found to be identifiable with any of the absorption spectra of the known visual pigments (Dartnall, 1952). The tripartition of the sensitivity data, moreover, does not completely harmonize with Le Gros Clark's correlation between the visual sensation in man and the lamination of the lateral geniculate body in other primates. Lastly, Granit's belief (1947) that the human periphery may be very similar in its properties to that of the cat, while supported by some (Weale, 1953), is not confirmed by the present data.

The only link between these and any other results consists in the tripartition of the foveal and peripheral sensitivities and the dichromacy of the colour vision accompanying them. Now the peculiar point common to all the proposed correlates mentioned in the Introduction—namely the retinal structure, the lamination of the lateral geniculate body, the structure of the visual cortex, the absorption spectra of photosensitive substances—is that they are essentially static factors. If the visual act is mainly of a dynamic nature, these factors will be unable to give any but the most superficial correlation because they imply a state of equilibrium. The dimension of time is not considered. Granit conceives modulation as something temporally static. If, however, a temporally variant element were to contribute to the process of vision none of the factors here mentioned could provide it *per se*. Only a neural mechanism can step into the breach: but the mode of its action remains to be elucidated. Thus the failure to achieve the expected correlations between peripheral colour vision and other attributes of the visual mechanism is probably due to the same reason as applies to the fovea: it would appear that they can be carried out only when all the non-sensory links in the visual chain are forged.

SUMMARY

1. The spectral sensitivity and wave-length discrimination have been measured at retinal eccentricities of 25, 45 and 70°. The test fields subtended at the eye an angle of 50′. Two luminance levels, 1·5 and 100 e.f.c. were used.

2. The fact that sensitivity data obtained with small fields exhibit enhanced sensitivity in three spectral regions—in the orange, green, and blue or violet respectively—in retinal locations of 0, 10, 15, 25, 45 and 70° suggests that three principal spectral mechanisms are present all over the retina.

3. The apparent incompatibility of this finding with the red-green confusion observed in wave-length discrimination measurements is discussed.

4. Wald's explanation of the improved sensitivity at high frequencies (short wave-lengths) in extra-foveal regions as being due to the absence of macular pigment is thought to be inadequate. An improvement in the receptor sensitivity of the peripheral as compared with the central retina is suggested as being an important contributory factor.

5. Parallels are sought between colour vision on the one hand and retinal structure and location on the other.

6. A comparison is made between the sensations due to spectral stimuli as seen foveally and peripherally respectively.

I should like to thank Mr S. E. Veronique for his help in recording the measurements.

REFERENCES

ABNEY, W. (1913). *Researches in Colour vision and the Trichromatic Theory.* London: Longmans, Green and Co.

CLARK, W. E. LE GROS (1949). The laminar pattern of the lateral geniculate nucleus considered in relation to colour vision. *Docum. ophthal.* **3**, 57–64.

DARTNALL, H. J. A. (1952). Visual pigment 467, a photosensitive pigment present in tench retinae. *J. Physiol.* **116**, 257–289.

GILBERT, M. (1950). Colour perception in parafoveal vision. *Proc. phys. Soc. Lond.* B, **63**, 83–89.

GRANIT, R. (1947). *Sensory Mechanisms of the Retina.* London: Oxford University Press.

HARTRIDGE, H. (1947). The visual perception of fine detail. *Philos. Trans.* B, **232**, 519–671.

HARTRIDGE, H. (1949). *Recent Advances in the Physiology of Vision.* London: Churchill.

HECHT, S. (1921). Photochemistry of visual purple. The kinetics of the decomposition of visual purple by light. *J. gen. Physiol.* **3**, 1–13.

HOLMES, G. (1945). The organization of the visual cortex in man. *Proc. Roy. Soc.* B, **132**, 348–361.

HUNT, R. W. G. (1950). The effects of daylight and tungsten light-adaptation on colour-perception. *J. opt. Soc. Amer.* **40**, 362–371.

HUNT, R. W. G. (1952). Light and dark adaptation and the perception of colour. *J. opt. Soc. Amer.* **42**, 190–199.

LYTHGOE, R. J. (1931). Dark adaptation and the peripheral colour sensations of normal subjects. *Brit. J. Ophthal.* **15**, 193–210.

MÜLLER, G. E. (1930). Über die Farben-empfindungen. *Z. Psychol.* Suppl.

MÜLLER, H. (1856). Anatomisch-physiologische Untersuchungen über die Retina des Menschen und der Wirbelthiere. *Z. wiss. Zool.* **8**, 1–122.

ØSTERBERG, G. (1935). *Topography of the Layer of Rods and Cones in the Human Retina.* Copenhagen, Nyt Nordisk Forlag: Arnold Busck.

PARSONS, J. H. (1924). *Colour Vision.* Cambridge University Press.

POLYAK, S. L. (1941). *The Retina.* University of Chicago Press.

RÖNNE, H. (1915). Zur Theorie und Technik der Bjerrumschen Gesichtsfelduntersuchung. *Arch. Augenheilk.* **78**, 284–301.

STARLING, E. H. (1949). *Principles of Human Physiology.* London: Churchill.

STILES, W. S. & CRAWFORD, B. H. (1933). The liminal brightness increment as a function of wavelength for different conditions of the foveal and parafoveal retina. *Proc. Roy. Soc.* B, **113**, 496–530.

THOMSON, L. C. (1946). Foveal colour sensitivity. *Nature, Lond.*, **157**, 805.

THOMSON, L. C. (1949). The influence of variations in the light history of the eye upon the course of its dark adaptation. *J. Physiol.* **109**, 430–438.

THOMSON, L. C. (1951). The spectral sensitivity of the central fovea. *J. Physiol.* **112**, 114–132.

THOMSON, L. C. & WRIGHT, W. D. (1947). The colour sensitivity of the retina within the central fovea of man. *J. Physiol.* **105**, 316–331.

TRENDELENBURG, W. (1904). Über die Bleichung des Sehpurpurs mit spektralem Licht in ihrer Abhängigkeit von der Wellenlänge. *Zbl. Physiol.* **17**, 720–724.

WALD, G. (1949). The photochemistry of vision. *Docum. ophthal.* **3**, 94–137.

WALTERS, H. V. & WRIGHT, W. D. (1943). The spectral sensitivity of the fovea and extrafovea in the Purkinje range. *Proc. Roy. Soc.* B, **131**, 340–361.

WEALE, R. A. (1951*a*). Hue-discrimination in para-central parts of the human retina measured at different luminance levels. *J. Physiol.* **113**, 115–122.

WEALE, R. A. (1951*b*). The foveal and para-central spectral sensitivities in man. *J. Physiol.* **114**, 435–446.

WEALE, R. A. (1953). The spectral reflectivity of the cat's tapetum measured *in situ*. *J. Physiol.* **119**, 30–42.

WILLMER, E. N. & WRIGHT, W. D. (1945). Colour sensitivity of the fovea centralis. *Nature, Lond.*, **156**, 119–121.

WRIGHT, W. D. (1946). *Researches on Normal and Defective Colour Vision.* London: Henry Kimpton.